On a New Type of Nephridia found in Indian Earthworms of the Genus Pheretima.

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With Plates 6, 7 and 8 and three Text-figures.

Table of Contents.

1. Introductory.

Hitherto zoologists have recognised in Annelida in general and Oligochæta in particular two types of nephridial system,

namely—(1) the ordinary or meganephric kind, consisting of a relatively few large and separate nephridia, segmental in arrangement, which open separately to the exterior, and (2) the plectonephric or diffuse variety, in which the nephridia are numerous, of small size, and described as being connected with one another by a network of ducts possessing many openings on the surface of the skin.[1] The meganephric type is found in all Polychætes (a few with protonephridia in the adult but the majority possessing nephridia with nephrostomes opening internally into the cœlom), in all Echiuroids (with nephridial funnels opening into the cœlom internally), in most Hirudinea (always with nephridia closed at their internal ends, the funnels, where they occur, never opening into the nephridial canals), and in many Oligochætes (always with open nephrostomes). The plectonephric type, on the other hand, has been described only among Annelids in certain Oligochætes and Hirudinea (e.g. Pontobdella), and we must conclude from the descriptions available that in essential features it resembles the type of excretory system found in many Platyhelminthes (e.g. Trematodes), the sole difference being that in the latter group discrete nephridia are not present (the funnels only being represented by flame-cells), and the system of ducts rarely has more than one or two separate openings to the exterior. In both types of nephridial system, however, meganephric and plectonephric, the outer ends of the nephridia have, with but few exceptions, always been described as opening to the exterior viâ the skin.

While undertaking the accurate anatomical description of one of the commonest Indian earthworms, Pheretima posthuma (L. Vaillant), supposed to possess a typical plectonephric type of nephridial system, I ascertained that no existing description applied to the condition of things found in this species; in fact, assuming existing descriptions of the plectonephric nephridial system to be correct, the only course to adopt is to consider the nephridial system of Pheretima posthuma and other species as a distinct third type of

[1] Cf. Sedgwick's 'Text-book of Zoology,' vol. i, pp. 498–502.

nephridial system which is here described for the first time. Since the essential feature of this third type is that, apart from the microscopic integumentary nephridia which open through the skin, all the numerous septal and pharyngeal nephridia are connected with a system of ducts, which open, not on the surface of the skin, but into the intestine and other regions of the gut (buccal cavity and pharynx), I propose to distinguish this type of nephridial system by the term "enteronephric" suggested to me by Dr. Woodland.

Before proceeding to describe this "enteronephric" type of nephridial system, I will provide a brief historical summary of previous descriptions of the plectonephric type so far as these are known to me from the very limited library resources available in the United Provinces.

I may add here that I am deeply indebted to Dr. W. N. F. Woodland, Professor of Zoology at the Muir Central College, Allahabad, for the keen interest he has all along taken in my work. He has made valuable suggestions, and also found time to read through and correct the manuscript of this paper. My grateful acknowledgments are also due to my professor Lt.-Col. J. Stephenson, D.Sc., Principal, Lahore Government College, for acquainting me with the literature on the subject and sending me nicely preserved specimens of different species of earthworms, and also for his constant encouragement given to me.

Both Dr. Woodland and Col. Stephenson have examined my slides and other preparations and have confirmed all my more important statements. I have their permission to mention this fact.

2. Historical.

The earliest statement concerning a nephridial system of a kind different from the ordinary meganephric was made by Perrier, references to whose work and that of other previous writers are given by Beddard (**3**, 1895), from whose account I quote. It is noteworthy that Perrier described his new type of nephridial system in Pheretima posthuma, the

species I have investigated in the present paper. Perrier states that the nephridia in this earthworm—"sont ici très rudimentaires, ce qui concorde avec l'absence d'orifice extérieur attribuable à ces organes." Beddard (**2**, 1888), however, found a large number of external excretory pores (nephridiopores) in Perichæta (Pheretima) aspergillum, and remarked that the nephridia formed numerous tufts of glandular tubules closely connected with the body-wall and the septa. Moreover, he did not regard the nephridia as rudimentary as Perrier did, but believed that they were in a very archaic condition. He emphasised two points in connection with these nephridia of Perichæta, which are, "firstly, that there is a connection between the nephridia of successive segments, and secondly, that the nephridial system of Perichæta consists of a network of tubules, the connection between the nephridial tufts of successive segments being brought about by numerous tubules which perforate the intersegmental septum." Beddard figures this network of tubules on the inside of the body-wall of Perichæta aspergillum (reproduced by Sedgwick, **13**, vol. i, p. 501). He also states in his paper that there is a very much greater number of nephridial pores in the anterior segments as compared with the posterior—a feature we shall refer to when considering the integumentary nephridia (vide infra). We may also note here in passing that it is fairly easy to see the external excretory pores in Pheretima posthuma by stripping off a portion of cuticle and examining it under the microscope, and that Perrier was certainly mistaken in recording an absence of nephridiopores in this earthworm.

Perrier's statement with regard to the position and distribution of nephridia in Perichæta robusta, which applies, according to my observations, equally well to Perichæta posthuma, is as follows: "Les organes segmentaires sous forme de tubes extrêmement délicates, sont adhérents aux cloisons, ou disséminées sur la membrane péritonéale que tapisse la cavité générale." In Pheretima posthuma also we can similarly recognise septal and integumentary

nephridia according as they are attached to the intersegmental septa or are adherent to the peritoneal membrane lining the inside of the body-wall; further, the two kinds differ considerably in size though alike in structure. This distinction between the integumentary and the septal nephridia does not seem to have been recognised by the earlier observers.

Just as Beddard (**2**, 1888), described the nephridial system of P. aspergillum as consisting of a network of tubules, similarly Perrier, also in giving a résumé of the anatomy of the group, regarded the nephridial system as forming a "réseau glandulaire," which appeared to him to be an indication of an incomplete suppression of these organs. Beddard (**1**, 1885), described eight nephridial tufts in each segment of Octochætus multiporus, and also later on recorded a very large number of orifices on the skin connected with these tufts. Benham found a large number of small and separate nephridia in a species of Perichæta, and Spencer (**14**, 1888), described in Megascolides australis "a network of small tubes with many external pores." This type of excretory system formed of small tubes was called "plectonephric" (plecto, I weave) by Benham, and Beddard described it as "diffuse." The essential idea associated with these terms was that of a network, and Beddard (**3**, 1895), speaking of this diffuse type of excretory system, says: "The delicate ramifying tubules especially attached to the septa can hardly be missed, at any rate in well-preserved specimens; . . . in the Perichætidæ the network is more diffuse and not broken into separate masses." At another place, writing of the "integumental nephridial network" of the Eudrilidæ, Beddard states that these tubes do not seem to be comparable to the "cœlomic network" of Perichæta, etc. He thus differentiates between an "integumental network," which is formed in the substance of the body-wall, and which he figures for Libyodrilus in his monograph (**3**, 1895), and a "cœlomic network," which is found on the peritoneal membrane lining the inside of the body-wall, and which is figured for Perichæta (after Beddard) by Sedgwick in his

text-book (**13**, 1898, p. 501). We may also mention here that the "integumental network" occurs in forms (Eudrilidæ) with paired meganephridia, while the term "cœlomic network" is a synonym for the "plectonephric" type of nephridial system.

The earlier observers, therefore, considered the nephridia in question as forming a sort of diffuse network which opened to the exterior by many excretory pores on the skin, and communicated with the body-cavity by means of funnels which were present in some tubules while absent in others. Although Benham found in a species of Perichæta a large number of small and separate nephridia, still the current idea of a "network" was essentially associated with these so-called "diffuse" nephridia.

More recently, however, Beddard seems to have abandoned the terms "diffuse" and "plectonephric," since writing as recently as 1910 (**4**), he describes these nephridia as a "mass of tubules which cover the inside of the body-wall and open to the exterior by innumerable openings," and he expresses a doubt concerning their supposed reticular connections in the following words: "It is at present uncertain whether these minute tubes are connected among themselves, thus forming a network passing through the septum, or whether each tube is isolated among its fellows, and forms a distinct nephridium, of which there are many in each segment, and entirely separate." He does not even mention here the terms "diffuse" or "plectonephric." Later still, in 1912 (**5**), Beddard uses the terms "micronephridia" and "meganephridia" when describing the two kinds of nephridia in earthworms, and not "meganephric" and "plectonephric," and it would appear from his account that he regards the nephridia as discrete structures quite distinct from one another.

From a developmental point of view these nephridia were not universally believed to be "plectonephric." The origin of the micronephridia was first elucidated by Vejdovsky (vide Thomson, **17**, 1892) in Megascolides australis; according

to him there is at first one simple "anlage" on each side in each segment which breaks up into separate loops, each loop becoming a separate micronephridium, without funnel (the original single funnel degenerates), and opening to the exterior. Bourne (7, 1894), found a similar development for Mahbenus imperatrix, and both Bourne and Vejdovsky are at one in denying any secondary communication between the separate nephridia. Meisenheimer (8), in 1910, denied the existence of a network altogether. He says: "Auffassung eines plectonephrischen oder diffusen Typus von Nephridien . . . wie er aber wohl hier bei den Regenwurmern in Wirklichkeit nicht besteht."

For comparison with the foregoing descriptions of the nephridia of Perichæta and allied types, I will here briefly summarise the results of my own observations on Pheretima posthuma. In the first place, these observations of mine have clearly disproved the idea of a reticulate system of ducts connecting nephridia of successive segments with each other; in other words, in the species I have examined the type of nephridial system is not plectonephric, though we may certainly retain the term "micronephric." In the second place, we can distinguish equally clearly three types of nephridia according to their size, arrangement, and place of opening of their ducts. These three kinds may be called (1) the septal, (2) the pharyngeal, and (3) the integumentary. Describing the integumentary first, we may briefly note that they are very minute structures, each of them quite separate and discrete, as was recognised by Benham. It is these only that open to the exterior viâ the skin. The septal nephridia are two to three times the size of the integumentary nephridia though similar in structure, and never open on the skin. They are also separate from one another, and are connected with a system of ducts which ultimately open medio-dorsally into the hypoblastic portion of the gut in a segmental manner. Lastly, the pharyngeal nephridia occur in bushy tufts around the œsophagus in three successive segments (fourth, fifth and sixth). Each tuft has a pair of ducts of its own, and these

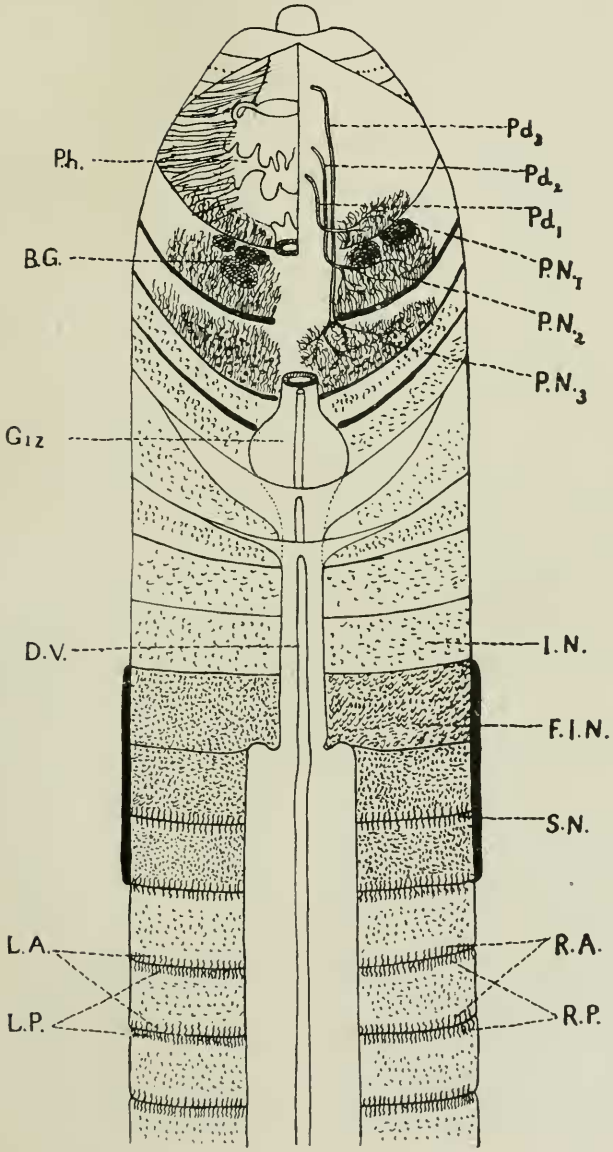
three pairs of ducts open into the buccal cavity and pharynx in the second and fourth segments.

Although it has long been recognised that in some Oligochætes certain nephridia do open into the alimentary canal, yet they have always been observed to open either into its anterior or stomodæal portion or into its posterior or proctodæal portion, and never into its intermediate or hypoblastic region. The former kind, i. e. those opening into the front end of the alimentary canal, have been called "peptonephridia" by Benham, and are known to occur in Enchytræidæ, Acanthodrilidæ, Endrilidæ, Cryptodrilidæ, and Geoscolecidæ. These are supposed to possess some peptic function, and hence the name. The pharyngeal nephridia of Pheretima posthuma may possibly belong to this category. The latter kind, i. e. those opening into the rectal end of the digestive canal, have been termed "anal" nephridia, and have so far only been found by Beddard in Octochætus multiporus and by Rosa (vide Spencer, **14**, 1906) in Allolobophora antipæ. But the septal nephridia of Pheretima are peculiar in the fact already stated, viz. that their ducts open medio-dorsally into the lumen of the hypodermal gut very nearly throughout its entire length in a regular segmental manner. Beddard (**3**, 1895), writing about the peptonephridia and anal nephridia, says that they never communicate with that section of the alimentary canal which is undoubtedly of hypoblastic origin. As my description in the following pages will prove, this assertion does not apply to the septal nephridia of Pheretima.

Text-fig. 1.

The general plan of the nephridial system in Pheretima posthuma. *S.N.*, septal nephridia; *I.N.*, integumentary nephridia; $P.N._1$, $P.N._2$, $P.N._3$, the pharyngeal nephridia of the fourth, fifth, and sixth segments; *F.I.N.*, "forests of integumentary nephridia; $Pd._1$, $Pd._2$, $Pd._3$, ducts of the pharyngeal nephridial nephridia of the fourth, fifth, and sixth segments; *R.A.*, *R.P.*, right anterior and right posterior series of septal nephridia; *L.P.*, *L.A.*, left posterior and left anterior series of septal nephridia; *B.G.*, blood-glands; *Ph.*, pharynx; *Giz.*, gizzard; *D.V.*, dorsal vessel. × 4.

TEXT-FIG. 1.



3. The Nephridial System of Pheretima posthuma.

(a) The General Plan of the System.

The nephridial system of Pheretima posthuma (Text-fig. 1) consists of three sets of tubules, each with its own system of ducts. (1) The first comprises the septal nephridia (*s.n.*), i. e. those which are attached to both sides of each of the intersegmental septa; these are the most important and the largest. They are regularly arranged on each septum throughout the length of the worm behind the fifteenth segment. These nephridia do not open on the skin, but in each segment discharge their excretory matter into a pair of septal excretory canals (*s.e.c.*, Pl. 6, fig. 1) situated on each septum, which in their turn empty themselves into a pair of supra-intestinal excretory ducts (*si.e.d.*, Pl. 6, fig. 1), which, running longitudinally along the dorsal side of the intestine, open medianly, at segmental intervals, into the intestinal lumen (Pl. 8, figs. 8 and 9).

(2) The nephridia of the second set lie just external to the œsophagus in the fourth, fifth and sixth segments, and in virtue of the place of opening of their ducts are called the pharyngeal nephridia (*P.N.*$_1$, *P.N.*$_2$, *P.N.*$_3$, Text-fig. 1). They occur as paired tufts lying at the sides of the œsophagus in each of the three segments named, and are closely intermingled with follicles of "blood-glands" which are also situated in these segments. The little ductules of individual nephridia in these bunches unite together at intervals, and ultimately form a pair of long, narrow muscular ducts (*Pd.*$_1$, *Pd.*$_2$, *Pd.*$_3$, Text-fig. 1) in each of these three segments. These three pairs of ducts run forwards ventro-laterally to the œsophagus and pharynx, and open into the buccal cavity and pharynx in the second and fourth segments.

(3) The nephridia of the third set, which are very much smaller in size than the septal nephridia and are adherent to and scattered over the inner surface of the body-wall (cœlomic epithelium), are described as "integumentary" nephridia (*i.n.*, Text-fig. 1). They are present in all the

segments of the worm except the first two, and they co-exist with the septal nephridia behind the first fifteen segments. Each of these nephridia opens separately to the exterior on the body-wall through a nephridiopore (Pl. 7, fig. 7).

(b) The Septal Nephridia.

(1) Position and Distribution.—The septal nephridia are attached, as their name implies, to the intersegmental septa near their outer margins close to the place where the septa join the body-wall. The septa of the first fifteen segments do not bear any nephridia, the first septum having nephridia attached to it being the septum 15/16. Behind this all the septa bear nephridia, although as we approach the posterior end of the worm the number of nephridia on each septum decreases. Each septum has nephridia attached to it on both its anterior and posterior surfaces. In a freshly-killed worm the septa present to the naked eye a shaggy appearance, and one can easily see with a hand-lens white fluffy masses attached to the septa, which are the septal nephridia. If, in a well-preserved specimen, a septum be cut off as closely as possible to the body-wall, the nephridia are also detached, since, as already stated, they are adherent to the septum. They can then be examined, along with the septum, under the microscope. On being examined under these conditions the nephridia are found to be attached to each septum in four linear series, two series being attached to the right half and the other two to the left half of each septum. The two series on each half of a septum consist of one series attached to the anterior surface of the septum and the other series to the posterior surface, i.e. an anterior and a posterior series. Each septum will therefore bear four series of nephridia (Text-fig. 1). (1) Right anterior (*R.A.*), (2) right posterior (*R.P.*), (3) left anterior (*L.A.*), and (4) left posterior (*L.P.*). As we shall see later on, the anterior and posterior series of nephridia of each half of a septum, right or left, are connected with a common duct, and therefore, on morphological grounds, we group together the anterior and

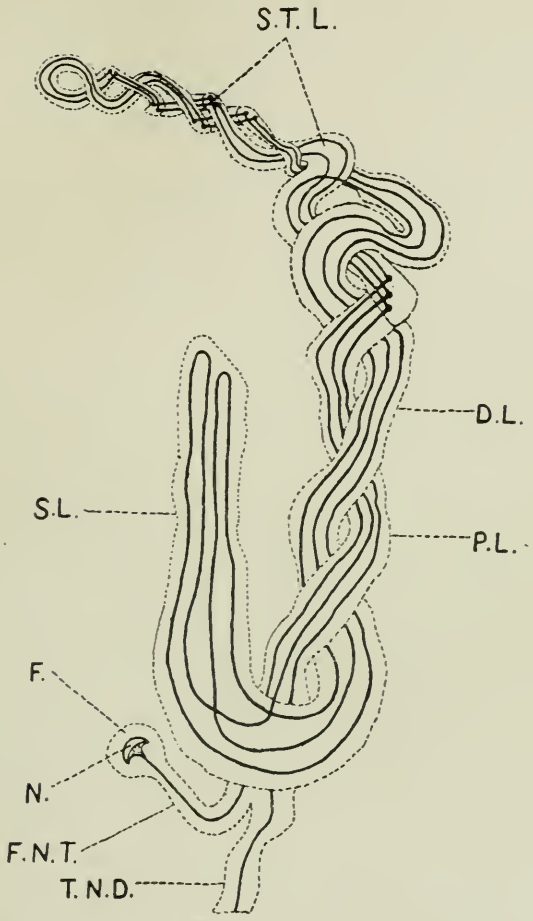
posterior series of nephridia of the right side as forming a distinct set separate from the similar series of the left side, which form another distinct set. The nephridia extend round the periphery of each septum from near the mid-ventral line of the worm almost to its mid-dorsal line.

(2) Attachment.—The line of attachment of the nephridia on each septum lies just external and parallel to the dorso-lateral vessel (the so-called "septal loop"). This blood-vessel, which plays a great part in the blood-supply of these nephridia, runs along the posterior face of each septum very near and parallel to its outer edge, i. e. the edge joining the body-wall. Each series of nephridia on each side of the septum, right or left, forms a single row with a line of attachment almost parallel to the septal loop.

(3) Number.—The number of nephridia on each septum varies within limits. On an average, there are 20 to 25 anteriorly and the same number posteriorly on each half of a septum (right or left). Each septum will thus have 40 to 50 nephridia on its anterior face and the same number on its posterior face, so that in a single cœlomic compartment we shall have 80 to 100 septal nephridia.

(4) Individuality.—Each nephridium is a minute but separate and discrete structure and there is no network of any kind connecting one nephridium with the other. Beddard (3, 1895) is thus certainly mistaken when he speaks of the excretory system of Perichæta as a "cœlomic network"; and also we cannot employ the terms "diffuse" or "plectonephric" in describing these nephridia. The idea of a reticular connection between these nephridia was probably due in the first place to the excessive minuteness of these structures, and secondly, to the fact that Pheretima and other tropical worms were unobtainable in a fresh condition by the European observers who described them. In the case of minute structures like these nephridia reliable observations cannot be made unless proper methods of fixation have been employed, and this was probably not the case with the worms examined by Beddard and others.

TEXT-FIG. 2.



A septal nephridium showing the course of the nephridial tube in it (diagrammatic). The dotted line represents the outline of the nephridium and the thick black line the nephridial tube. *F.*, funnel; *F.N.T.*, the free first part of the nephridial tube; *N.*, nephrostome; *S.L.*, the short, straight lobe; *P.L.*, the proximal limb, and *D.L.*, the distal limb of the twisted loop; *T.N.D.*, the terminal nephridial duct going to the septal canal; *S.T.L.*, the spirally twisted loop. × 276.

(5) Outline Structure and Topography of a Nephridium.—Each nephridium (Text-fig. 2) consists of (i) a funnel (*F.*) followed by a short narrow tube (*F.N.T.*), which is bent on itself before joining the body of the nephridium, (ii) the main body of the nephridium consisting of a short straight lobe (*S.L.*) and a long spirally twisted loop (*S.T.L.*). The straight lobe is rounded at its free end, and is continued at its other into one of the limbs of the long twisted loop, which is more than twice the length of the straight lobe, and (iii) a terminal nephridial duct (*T.N.D.*), which is a continuation of the other limb of the twisted loop and leads from the nephridium to the septal excretory canal.

Unlike the case in Lumbricus and Megascolides, the whole nephridium in Pheretima posthuma lies within the bounds of a single segment; in other words, it does not extend over two segments as in Lumbricus, and we do not distinguish here, therefore, a pre-septal portion of the nephridium from the post-septal portion. Beddard (**3**, 1895) says—"The nephridia are always much-coiled tubes, and they always occupy two segments, and two segments only. The internal aperture, the funnel, lies a segment in front of that which bears the external pore." He seems to regard the fact of a nephridium extending over two segments as an essential feature in the disposition of the nephridia of earthworms, and it is therefore a novel fact that in Pheretima a nephridium, including its funnel and all other parts, lies wholly within the boundaries of a single segment. Another feature already stated, and which we shall return to later in detail, is that the septal nephridia do not open directly to the exterior as they do in Lumbricus. They open, as already described, into the septal excretory canal, and that is why we have not got in Pheretima a series of nephridiopores arranged segmentally on the body-wall as we have in Lumbricus.

In brief, the whole nephridium, including its funnel, hangs freely in the cœlomic cavity, and is solely attached to the septum near its outer edge by means of the terminal nephridial

duct, which runs along the septum obliquely to join the septal excretory canal (Pl. 6, fig. 1).

(6) The Minute Structure of a Single Nephridium. —Leaving aside the funnel, the first part of the nephridial tube and the terminal nephridial duct, the remaining part of each nephridium consists of a tube coiled into several loops closely bound together by membrane richly supplied with blood-vessels. The detailed account of the structure of the three parts of a nephridium is given below.

(i) The funnel (Pl. 7, figs. 3, 4 and 5). Each nephridium commences with a minute bulb-like swelling, the funnel, which has a transversely oval opening, the nephrostome (*N.*), on its ventral side. The funnel when looked at under the high power of the microscope appears slightly reniform in shape rather than rounded, and measures 28 μ in its shorter and 39 μ in its longer diameter, while it is about 15 μ in thickness dorso-ventrally.

The funnel is a two-lipped (bilabiate) structure with its upper lip of the shape of a hood; this lip is very large and prominent in comparison with the lower lip, which is very small and simple. The body of the upper lip is formed of a single large semicircular cell known as the central cell bounded by a number of marginal cells. The central cell occupies the centre and lower half of the upper lip, and has a large and prominent rounded nucleus in its centre. The outer margin of the central cell is beset with eight or nine marginal cells each with a rounded nucleus in it. All the marginal cells are equal in size, and are set in an incomplete circle round the terminal aperture of the funnel, i.e. the nephrostome, forming the margin of the upper lip. The marginal cells are profusely ciliated over the whole of their centrally directed face; the cilia are pretty long and closely set, and in whole preparations are seen to surround the top of the funnel like a halo, while in sections (Pl. 7, fig. 4) they present a characteristic bushy appearance.

The lower lip, which is not so thick as the upper, has a slightly convex border, and is made up of four or five cells,

each with a deeply-staining, small elliptical nucleus. These "cells" form a compact structure, and no boundaries can be seen separating them from one another, their number being inferred from the number of nuclei. The lower lip also, like the upper, bears cilia. The actual terminal opening between the two lips, viz. the nephrostome, is, as already stated, transversely oval, and measures about 15 μ from side to side and about 9 μ dorso-ventrally. A number of cœlomic epithelial cells invest the funnel here and there.

In order to ascertain the distribution of cilia in the funnel, the latter should be examined in the fresh state when the cilia are active. If nephridia from a freshly-killed worm are examined in salt solution (·75 per cent.), the cilia are most evident in funnels which are either seen in profile or have their ventral sides uppermost. The cilia are arranged along eight or nine lines which radiate from the nephrostome or mouth of the funnel to the periphery, each line of cilia corresponding to one marginal cell. All the cilia of each line beat simultaneously towards the mouth of the funnel but alternate in movement with the cilia of the neighbouring lines. All the cilia are of the same length, and of course serve to drive the excretory matter of the cœlom into the nephrostome.

The funnel of the nephridium of Pheretima posthuma is much simpler in structure than that of Lumbricus. It is much smaller in size in accordance with the very small size of the nephridium as a whole. The central cell resembles that of the funnel of Lumbricus, but the number of marginal cells is very small, while there are no gutter-cells, so far as I can make out. Curiously enough I have never seen the "débris" of cœlomic corpuscles on the funnel of Pheretima, which fact is remarkable, since this débris is described by Benham as being a constant feature in the funnel of Lumbricus.

The funnel of P. posthuma also differs from that of Perichæta malamaniensis, described by Benham (**6**, 1891); in the latter there is no central cell, and the ciliated

marginal cells form a complete circle round the terminal aperture of the funnel.

(ii) The Main Body of the Nephridium. As already stated, the body of a nephridium comprises a short, straight lobe and a long spirally twisted loop (Text-fig. 2). The straight lobe is, on an average, about 225 μ in length and 45 μ in thickness, while the twisted loop is 480 μ in length, i. e. more than twice the length of the straight lobe. The straight lobe is free and rounded at its one end, while at its other it is continued into one of the limbs (distal) of the twisted loop. The latter consists of two limbs, a proximal and a distal, spirally twisted about each other, the number of spiral twists in the loop varying from nine to thirteen (Text-fig. 2).

The funnel, together with the first part of the nephridial tube which immediately follows the funnel, is generally situated towards the side of the straight lobe away from the twisted loop. This commencing part of the nephridial tube is free for a short distance, but soon bends, to become incorporated into that limb of the twisted loop which I have called the proximal (*P.L.*, Text-fig. 2), to distinguish it from the other or distal limb (*D.L*), which is continuous with the short, straight lobe.

The nephridial tube, having entered the proximal limb of the twisted loop at its base, continues in that limb right up to the top of the loop, where it curves round, and then follows its course into the distal limb. On reaching the base of the distal limb the tube runs into the straight lobe, in which it goes to the top of the lobe, loops backwards, and then, passing through the base of the lobe, enters into the distal limb again. Here it runs parallel to its first course though in the reverse direction, and on reaching the top of the loop it bends round and runs backwards in the proximal limb until it has reached its base just about the point (*X*, Pl. 7, fig. 2), where the nephridial tube first enters the body of the nephridium. From this place (*X*, Pl. 7, fig. 2), in the base of the proximal limb the tube crosses over to the base of the straight lobe and there

makes another loop similar and parallel to the first, after which the tube runs into the distal limb once again, i. e. a third time. This time it does not go right up to the top of the limb, but having gone only half the length of the limb, loops back to enter the proximal limb also a third time, and then runs towards the base of the nephridium, and is continued outside the body of the nephridium as the terminal nephridial duct.

The exact course of the tube in the nephridium can easily be followed by reference to the accompanying diagrams (Text-fig. 2 and Pl. 7, fig. 2). We may note, however, that there are, in all, three parallel tubes in each of the two limbs of the twisted loop in their lower halves, while there are only two in each in their upper halves: consequently the top halves of the two limbs are thinner than the basal halves, and the straight lobe has two loops of tubes, i. e. four tubes running parallel in it. Of these two loops one is the outer or the first loop and the other the inner or the second; the inner (*i.l.*) lies towards the side of the lobe nearer the twisted loop, while the outer (*o.l.*) loop of the tube lies away from the twisted loop. We may also observe that the terminal part of the nephridial tube leaves the body of the nephridium just about the same place where the first part of the tube enters it. Moreover, the lumen of the tube is intracellular all along, the tube being composed throughout of hollow cells joined end to end like so many drain-pipes.

(iii) The Terminal Nephridial Duct (Text-fig. 2, *T.N.D.*). The terminal nephridial duct is a continuation of the proximal limb of the twisted loop running towards the septum. Soon after leaving the nephridium it becomes attached to the septum near its outer margin just external to the dorso-lateral vessel. From this place of attachment on the septum the terminal nephridial duct runs inwards and upwards along the septum, following an oblique course (Pl. 6, fig. 1). During its course along the septum it crosses over the wall of the dorso-lateral vessel and then enters the septal excretory canal (vide infra). As the dorso-lateral vessel and the septal excretory canal lie on the

posterior face of each septum, the nephridial ducts of the posterior nephridia join the septal canal without having to pierce the septum, while the ducts of the anterior nephridia generally pierce the septum and come over to the posterior surface before crossing the dorso-lateral vessel. The crossing of the dorso-lateral vessel (*dl.v.*, Pl. 7, figs. 6 and 7), therefore, almost always takes place on its posterior wall, but I have also come across in sections a certain number of cases where the nephridial ducts of the anterior nephridia cross the dorso-lateral vessel along its anterior wall and then pierce the septum to join the septal excretory canal. Thus we meet with two conditions : either the septum is pierced through before the dorso-lateral vessel is crossed over along its posterior wall, or it is pierced after the vessel has been crossed over along its anterior wall ; of these the former is the rule, while the latter is only an exception.

The nephridial ducts from their point of attachment to the septum to the point where they enter the septal excretory canal are 412 μ to 825 μ in length ; they become longer as we go to the dorsal side of the animal.

(7) The Ciliation of the Nephridium.—As regards the cilia lining the nephridial tube (Pl. 7, fig. 2), we have to note that they are not distributed uniformly all along its length, but are confined to certain definite regions. I can confidently state that there are at least four ciliated tracts along the course of the nephridial tube. The first tract extends from the funnel to the point where the first free part of the nephridial tube enters the base of the proximal limb of the twisted loop (*a* to *a'* in Pl. 7, fig. 2). Both the second and third ciliated tracts lie in the short straight lobe. As already stated, there are four parallel tubes in this lobe, which go to form the two parallel loops, the outer and the inner (*o.l.* and *i.l.*). There is a ciliated tract in each of the two loops. The second ciliated tract lies in the outer loop, and extends from the apex of this loop to more than half the length of the inner tube of the loop between the letters *bb'* ; the cilia in this tract are directed towards the base of the

straight lobe and so work in that direction. The third tract of cilia occurs in the inner loop in its proximal limb along the entire length of the latter between the letters *cc'*. This part of the tube is always brownish and semi-opaque, being full of excretory products; indeed, it is sometimes almost blackish in appearance. We might call the brownish portion the "brown ciliated tube," and note that the cilia in this region work upwards towards the apex of the straight lobe. The fourth ciliated tract lies in the terminal part of the nephridial tube, from the point where it leaves the nephridium to the point where it becomes attached to the septum, between the letters *d* and *d'* (Pl. 7, fig. 2).

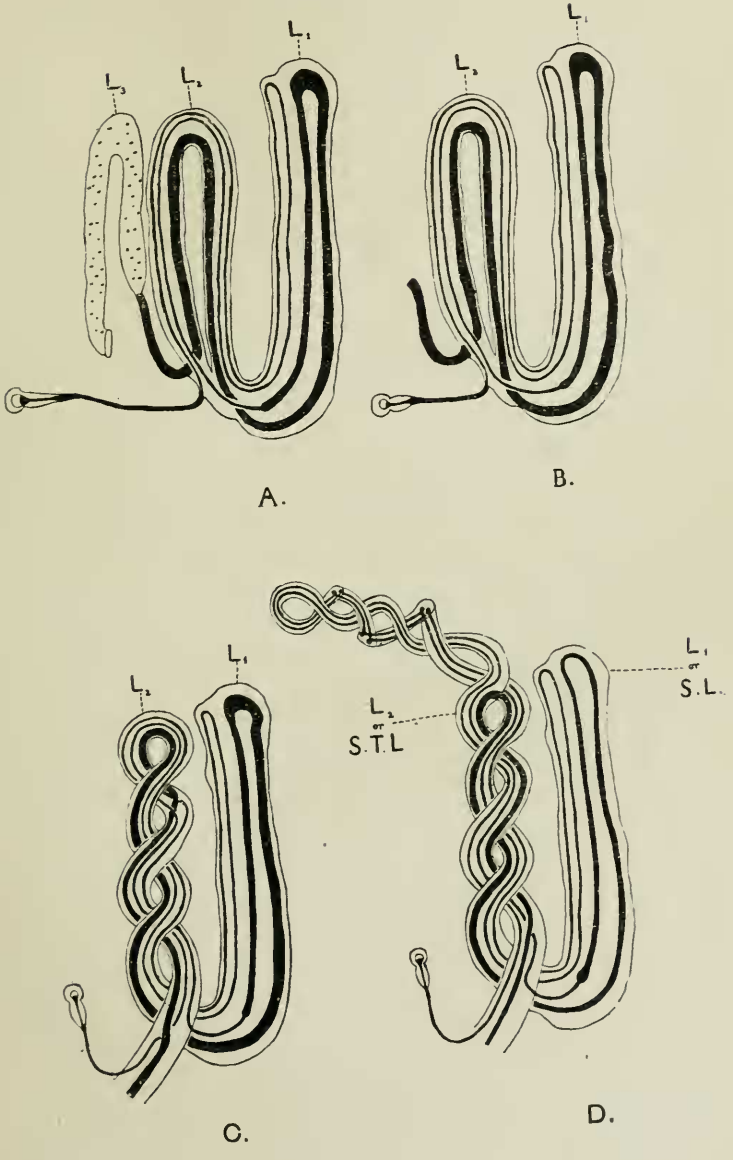
In each ciliated tract the cilia are disposed in a double row, and they move in such a manner as to produce along the axis of the tube a wavy movement closely resembling the flickering of the flagellum or "flame" in a proto-nephridium. (Pl. 7, fig. 2, gives a good idea of both the distribution of the cilia and the flickering movement produced by their action.)

(8) Comparison of the Nephridium of Pheretima with that of Lumbricus.—A comparison between the nephridia of Lumbricus and Pheretima reveals the interesting fact that the latter can be derived from the former by removing its muscular loop and spirally twisting the two limbs of the second loop and then lengthening them out. The accompanying series of diagrams serves to illustrate how the nephridium of Pheretima can be derived from that of Lumbricus.

TEXT-FIG. 3.

A series of four diagrams showing how the nephridium of Pheretima can be derived from the nephridium of Lumbricus. *A* is a diagram of the nephridium of Lumbricus showing the "first" and the "second" loops and the "muscular loop." In *B* the muscular loop is omitted, but the rest is the same as *A*. In *C* the two limbs of the second loop are twisted about each other, forming four twists. In *D* the twisted loop is lengthened out and the resultant is a diagram of a septal nephridium of Pheretima. L_1, the first loop; L_2, the second loop; L_3, the muscular loop; *S.T.L.*, the spirally twisted loop corresponding to the second loop of Lumbricus; *S.L.*, straight lobe corresponding to the first loop in *A*, *B* and *C*.

TEXT-FIG. 3.



(c) The Ducts and Openings of the Septal Nephridia.

(1) The Septal Excretory Canal (*s.e.c.*, Pl. 6, fig. 1).—The septal canal is a prominent channel running along the posterior face of each septum near its outer border, and, as previously stated, lies internal and parallel to the dorso-lateral vessel along its entire course. There is a pair of these septal excretory canals on each septum—one on each half, right and left. In preparations of the septa in which the outer edge is not injured one can easily see a canal beginning from the ventral side and running internal to and alongside the dorso-lateral vessel ; it is generally narrower in diameter than the blood-vessel and has the appearance of being empty or containing a colourless fluid, while the blood-vessel is coloured yellowish owing to the presence of blood ; the one can thus be easily distinguished from the other.

The septal canal originates ventrally on each side, right and left, by the union of a few (three or four) of the ducts of nephridia lying in the ventral region. In complete preparations of septa it is easy to demonstrate the commencement of this canal by the union of three or four branches, each of which itself has been formed by the union of several nephridial ducts. The place of commencement of this canal, or rather the place where several branches meet to form this canal, is situated a little higher or dorsal to the place where the dorso-lateral vessel receives a septo-intestinal branch from the intestine (*si.v.*, Pl. 6, fig. 1). The septal excretory canal after its formation runs dorsalwards, as already described, alongside the septal loop, the space separating these two being usually equal to about half the thickness of the septal canal, but not uncommonly the walls of the two are in contact. The septal canal receives the ducts of all the nephridia, anterior and posterior, belonging to its own half of the septum, the nephridial ducts running a fairly long and oblique course before reaching the septal canal, and even after reaching it, many of them continue a short distance

alongside it before actually entering. As a rule, each nephridial duct opens separately into the septal canal, but at places one also comes across a nephridial duct emptying its contents into another nephridial duct instead of opening independently into the septal canal. In serial sections (Pl. 7, fig. 6) it is easy to follow a nephridial duct from the place where it leaves the nephridium and runs along the septum to cross the dorso-lateral vessel anteriorly or posteriorly to the place where it enters the septal canal.

On following both the dorso-lateral vessel and the septal excretory canal towards the dorsal side, we find that about the level of the dorsal wall of the gut, they (i.e. the septal canal and the dorso-lateral vessel) begin to diverge from each other; the dorso-lateral vessel bends inwards to join the dorsal vessel, and the septal excretory canal enters the supra-intestinal excretory duct of its own side (Pl. 6, fig. 1).

(2) The Supra-intestinal Excretory Ducts.—These are a pair of longitudinal ducts situated in the mid-dorsal line beneath the dorsal vessel and above the dorsal wall of the gut. They are closely attached to the dorsal wall of the gut, but can be separated by careful dissection. They are always very prominent structures in sections (Pl. 8, figs. 8, 9), and have all along been taken to be blood-vessels. Stephenson (15, 1913) mistakes them for a continuation of the supra-intestinal blood-vessel, and says: "The supra-intestinal vessel extends back along the œsophagus and intestine beneath the dorsal vessel, communicating with the hearts in the segments xii and xiii and with the alimentary plexus throughout its extent." At another place he adds: "The supra-intestinal vessel . . . exists only in certain of the anterior (œsophageal) segments of the body in the Tubificidæ; in Pheretima it extends backwards along the intestine also." As a matter of fact, the supra-intestinal vessel does not extend behind the thirteenth segment, since it terminates in that segment by joining the pair of hearts there. In the fourteenth and fifteenth segments there is no blood-vessel nor any other tubular structure, while behind the fifteenth segment we get the supra-

intestinal excretory ducts occupying the same relative position as that occupied by the supra-intestinal vessel in the anterior region. These excretory ducts begin from the septum 15/16 because this is the first septum which bears the septal nephridia. I myself believed these ducts to be blood-vessels for a long time and recorded them as such in my notes and drawings of the blood-system, and it was not until my attention was definitely directed to them by the discovery of their continuity with the septal canals that I recognised their true nature. It need hardly be said that these supra-intestinal ducts are never seen to contain blood, either in dissections or in sections; and they thus offer a striking contrast to the dorsal vessel, which is almost invariably gorged with blood.

The supra-intestinal ducts extend along the entire length of the gut from behind the septum 15/16 to the posterior end of the body of the worm. Anteriorly and posteriorly they become narrow and single, while in the region of the intestine they are always large and paired and, therefore, quite prominent structures. Just a little behind each intersegmental septum these two longitudinal ducts communicate with each other for a very short distance (30 μ), but otherwise the two are entirely separate although they lie side by side. In sections of a fair-sized worm, these channels in the region of the intestine between two intersegmental septa were about 115 μ in diameter, while the diameter of the dorsal vessel at that place was about 220 μ. As already mentioned, these supra-intestinal excretory ducts receive a pair of septal excretory canals in the region of each intersegmental septum, so that the excretory fluid from the septal canals is discharged at each intersegmentum into these paired channels, the longitudinal extent of which exactly coincides with the longitudinal distribution of the septal canals and the septal nephridia.

By what means do these supra-intestinal excretory ducts communicate with the exterior for the discharge of their contents? That was a problem which baffled me for many a month, and all attempts at finding an external opening of

these longitudinal ducts failed. With this purpose in view I especially examined these ducts at their two ends, anterior and posterior, but with no success, the ducts ending abruptly in those two regions without showing any signs of opening to the exterior. Next, since Beddard (3, 1895) has suggested a possible connection between the nephridia and the dorsal pores, I carefully examined my preparations to see if there was any communication between the supra-intestinal ducts and the dorsal pores, but I could find none.

Subsequently, however, while looking at a series of sections of the earthworm in the region of the intestine, I noticed that at one place one of the two supra-intestinal ducts communicated with the lumen of the gut by a distinct opening, and though at the time I concluded that this communication must be accidental in origin, yet it gave me the clue which ultimately led to the correct solution of this problem. Later, following up this clue, I prepared a complete series of sections passing through seven segments of the worm's intestine, and in this series I found exactly seven communications between one or other of the two supra-intestinal ducts and the lumen of the intestine. It thus became certain that these longitudinal excretory ducts did not open at all to the exterior but into the lumen of the intestine, the openings being arranged segmentally. In my serial sections it can be seen that in each septal region one of the two supra-intestinal excretory ducts, the right or the left, takes a dip into the dorsal wall of the gut on one side of the typhlosole, that this dip deepens, and that an actual communication is formed between the supra-intestinal duct and the lumen of the gut by means of a very short and narrow ductule (Pl. 8, figs. 8, 9). This narrow ductule is situated at the rounded corner in the gut where the base of the typhlosole passes into the gut epithelium, or, in other words, where the gut epithelium bends inwards to form the typhlosolar projection into the gut. The narrow ductule has muscular walls when traversing the muscle layers of the gut, but has a special lining of small epithelial cells where it pierces the gut epithelium. The ductule seems to be a

laterally compressed structure, elliptical in cross-section rather than circular, since in serial sections of the intestine the ductule measures certainly more than 6 μ in its longer diameter, as traces of the ductule can be seen both in front of and behind the single section which cuts completely through this ductule and which (the section) itself is 6 μ in thickness; while when we measure the width of the ductule in this very single section it is about 4·2 μ. The ellipsoid ductule, therefore, measures more than 6 μ in the longer diameter and 4·2 μ in the shorter diameter of its cross-section.

It is remarkable that these narrow ductules leading from the supra-intestinal ducts to the lumen of the gut are, in the first place, segmentally arranged, and in the second place, are so narrow and minute that they can easily be mistaken for cracks in the sections unless they are examined carefully. But in a series of sections passing through five or six segments one never fails to find these narrow ductules in each septal region. It is also interesting to note that if we remove the supra-intestinal ducts from a part of the intestine and examine them after suitable preparation, we are able to see an aperture on one or other of the ducts at each septal plane. These apertures, of course, mark the positions of the downwardly-dipping ductules, which have of necessity been torn off in the process of removal of the supra-intestinal ducts from the intestine.

The supra-intestinal ducts do not both communicate with the gut in each intersegmental place, but it is always only one of them—sometimes the right and sometimes the left—which does so. It might be thought that the right and the left supra-intestinal ducts communicate with the gut one behind the other in a regularly alternate manner, but this is actually not the case. In the series of sections passing through seven intersegmental places the ducts opened into the gut antero-posteriorly in the following order: Left, left, right, left, right, right, right. When either of them has communicated with the lumen of the gut it then communicates with the other supra-intestinal duct for a very short interval (30 μ generally),

and then the two separate again. At four places I observed these communications; they extended over five sections at each of these four places, each section being 6 μ in thickness, thus giving 30 μ as the width of the communication between the two longitudinal ducts. Since the two ducts communicate with each other soon after one of them has communicated with the gut, the order of opening of the duct of one side or the other into the gut mentioned above is evidently of no consequence.

We must therefore conclude that the excretory products in solution are discharged into the lumen of the gut, whence they are got rid of through the anus along with the fæces.

There are a few points with regard to the septal excretory system (enteronephric) to which I should like to draw attention. The first is its strictly segmental character. It has always been recognised that in earth-worms like Lumbricus the nephridia are segmental in arrangement, and, as a matter of fact, the old name for these structures was "segmental organs"—a term which emphasised their segmental distribution. Although this old name has been given up, still the metameric disposition of the nephridia in Lumbricus and other worms is clearly recognised; but Beddard (**3**, 1895,) writing of the nephridial system of Perichæta (Pheretima) in particular and the plectonephric type of nephridial system in general, says, "The segmentation so clearly visible in most of the organs of the worm's body has here been lost." This assertion, of course, was based on an imperfect knowledge of the nephridia of Pheretima. We now know that the nephridia of Pheretima are clearly segmental structures, since they are serially repeated on each septum behind the fifteenth segment; similarly are the septal canals strictly segmental, as we have a pair of them on each septum. Lastly, the openings of the pair of supra-intestinal ducts are also segmental, since we get one opening into the intestine in each intersegmental space. The whole of the enteronephric nephridial system is, therefore, arranged on a strictly segmental plan.

The multiple character and probable efficiency of these organs is another notable feature. Beddard (**4**, 1910) speaks of the exceeding activity of Perichæta as its distinctive feature. and adds: "Dr. Baird, in a communication to the Zoological Society, remarked upon the agile fashion in which these tropical Annelids will spring off a table when touched or any way interfered with. Gardeners have recognised this character and given it the name of eel-worm." In an active worm of this kind it would be necessary to have a very efficient excretory system. It has been suggested that in a worm in which the cœlomic fluid is constantly flowing from one end of the body to the other and vice versâ, in correspondence with the great activity of the animal, these small nephridia in large numbers, about a hundred or so in each segment, with an equal number of funnels and nephrostomes which would occupy every nook and corner of the segment, would be much more efficient than a single large nephridium with a single nephrostome. There can be no doubt whatever that these nephridia are active excretory organs, and that Perrier's view regarding them as rudimentary is certainly not tenable.

By far the most remarkable feature, however, of the septal nephridial system is the absence of any direct communication between the nephridia and the exterior, as we find in almost all other earth-worms. In Pheretima, on the other hand, we get instead a series of segmentally arranged communications between the nephridial system and the lumen of the intestine. This is entirely a new feature in the morphology of the excretory system of earth-worms, and has been recorded, so far as I know, for the first time in this paper.

(d) The Pharyngeal Nephridia and their Ducts.

The pharyngeal nephridia, as already stated, consist of tufts of these organs surrounding the œsophagus in Pheretima posthuma in the fourth, fifth and sixth segments. In the natural condition these tufts are hidden under the thick

septa which separate the fourth, fifth, sixth and seventh segments from one another, and which form a series of cones one inside the other around the œsophagus in these segments; one has, therefore, to remove these septa to a large extent in order to display the pharyngeal nephridia.

(1) Literature.—The pharyngeal nephridia were first described by Beddard in Octochætus. In this genus these nephridia consist of a single pair of tufted organs lying in contact with the pharynx, each tuft possessing a duct which runs forwards and opens into the buccal cavity. These tufted organs were called "salivary glands" by Beddard, and Benham gave them the name of "peptonephridia"—a term accepted by Beddard. Spencer in 1888 (**14**) described in Megascolides australis a large mass of minute tubules occupying most of the space between the pharynx and the body-wall. These tubules were said to be much-coiled structures identical with ordinary nephridia; further, the ducts of these nephridia-like organs appeared to have joined together at intervals to form a common duct, one on each side, and these common ducts opened into the pharynx, their openings having been identified in sections. Michaelson in 1913 (**9**) described a pair of peptonephridia lying lateral to the œsophagus in Periscolex, which were broadly swollen behind and passed in front into a long, narrow duct. Miss Raff (**11**, 1910) says: "A noticeable feature in the dissections of some of the species such as Megascolex dorsalis, Megascolex fielderi and Diporochæta tanjilensis, is the presence of a large number of nephridial tubes attached ventrally in the region of the pharynx. They are in the form of bunches, and have generally been considered as 'peptonephridia.' The latter have been defined by Beddard as nephridia opening into the anterior section of the alimentary canal and functioning in relation to digestion. So far, however, as I have examined, I have found them opening to the exterior, not into the canal; I cannot therefore regard them as peptonephridia, but simply as a specialised group of nephridia, the meaning of which is not clear." Powell (**10**, 1911–12) referred to the pharyngeal

nephridia in Pheretima posthuma, and described them as occurring in the fifth and sixth segments. He seems to have seen the cœlomic funnels of these nephridia, which answer in this and in all other respects to the definition of a nephridium morphologically. He says nothing about the course of the ducts and their openings, and is not certain about the function of these nephridia.

(2) Description of the Pharyngeal Nephridia in Pheretima posthuma.—Beginning from behind, we first come across these pharyngeal nephridia in the sixth segment (PN_3, Text-fig. 1). In a dissection from the dorsal side, after removal of the septum 6/7, the pharyngeal nephridia are seen as two large and conspicuous masses of nephridial tubules, one lying on each side of the œsophagus, and resembling, under a lens, a big tuft formed of a large number of strings. On careful examination, after cutting across and reflecting back the part of the œsophagus in the sixth segment, we find that these tufts extend around the œsophagus to the mid-ventral line. Dorsally they cover the greater part of the œsophagus, and also tend to encroach upon the dorsal vessel, which is, however, not covered by them. The paired tufts are thus disposed in two semicircular curves round the œsophagus, each curve extending from about the mid-dorsal to the mid-ventral line. Posteriorly these nephridial masses are loosely attached to the septum 6/7.

Intermingled with the nephridial tufts of this segment are found a large number of rounded cell-masses called the "blood-glands." These rounded structures are not aggregated into follicular spaces here as in the fifth segment (vide infra), but are dispersed among the nephridial tufts. The blood-glands as well as the nephridial tufts have a copious blood-supply, each nephridial tuft receiving a branch from the dorsal vessel, which divides and subdivides to supply blood to the individual elements of these tufts.

The ductules of the individual nephridia join with one another at intervals and form ducts which unite with other similar ducts and so on, and ultimately form a pair of long

thick-walled common ducts, one from each nephridial tuft. This pair of common ducts runs forwards, and can easily be seen on each side of the mid-ventral line about 2 to 3 mm. apart in the anterior part of the sixth segment. After traversing the sixth segment these ducts pierce the septa 5/6 and 4/5 in front and open finally into the buccal cavity about the middle of the second segment ($Pd._3$), quite in front of the region of the pharyngeal mass and the supra-pharyngeal ganglion. The openings of these ducts into the buccal cavity have been identified in sections and also verified by a minute dissection of this region.

The nephridial tufts of the fifth segment ($PN._2$) are considerable in size and agree in all essentials with those of the sixth segment. In this section also we have a number of blood-glands; they are, however, not diffuse, but are aggregated into two or more masses in the shape of follicles on each side which resemble bunches of red grapes in the fresh condition. The nephridial tufts here also lie on each side of the œsophagus and extend both dorsally and ventrally; they lie chiefly in the posterior half of this segment, but extend forwards also to cover partially the blood-glands which occupy the anterior half of this segment. It is also seen that some of the nephridia actually penetrate into the blood-glands. Like the nephridial masses of the sixth segment the nephridial tufts here also are connected with a pair of common ducts, one on each side, about 2·5 mm. apart. These ducts run forwards, penetrate through the septum 4/5, and enter the pharynx in the anterior part of the fourth segment, just a little in front of the middle line of setæ of this segment ($Pd._2$).

The third pair of nephridial tufts ($PN._1$) lies in the posterior part of the fourth segment attached to the anterior surface of the septum 4/5. These tufts consist of comparatively fewer nephridia than there are in the fifth and sixth segments. The pair of ducts from these tufts travels only for a short distance forwards, and opens into the pharynx in the posterior half of the fourth segment behind the middle line of setæ ($Pd._1$).

We have thus three pairs of nephridial tufts in the anterior region, a pair in each of the fourth, fifth and sixth segments. We have also three pairs of thick and muscular nephridial ducts, a pair to each pair of tufts, which open into the buccal cavity and the pharynx.

It will be seen that it is a matter of some difficulty to define accurately where the three pairs of ducts from the pharyngeal nephridia open. In a dissection of the first four segments it is difficult to determine the exact boundaries of successive segments, since there are no septa in these segments, the cœlomic cavity being continuous. I therefore made use of serial sections of this region to determine accurately the places of opening of these ducts. In these sections also the dorsal pores marking off one segment from another are absent, and so I had to use the ring of setæ in the middle line of each segment as my criterion for determining the boundaries of successive segments.

As regards the structure of each pharyngeal nephridium, we have to note that it is very similar to that of a septal nephridium. The pharyngeal nephridium also consists of a short straight lobe and a long spirally twisted loop, the proximal limb of the latter being continued out as the terminal nephridial duct. But I have never been able to see the "funnel" in these pharyngeal nephridia, in spite of repeated attempts, and have come to believe that it is absent. Powell (**10**, 1911–12), however, writing about these nephridial nephridia of Pheretima posthuma, says: "Under the microscope and with the aid of sections each of these strings is seen to be a tubular structure opening into the cœlom by a slightly funnel-shaped aperture bearing a ciliated epithelium." As I have already stated, I have not been able to see the "slightly funnel-shaped apertures" of these nephridia, and cannot therefore corroborate Powell's statement. In the short straight lobe the second and third ciliated tracts can easily be made out, and work in the same way and in the same direction as a septal nephridium; but I have not been able to make out the first and fourth ciliated tracts here. Whether

these nephridia are excretory in function or have a peptic function in connection with assimilation is still to my mind problematical.

(e) The Integumentary Nephridia.

The integumentary nephridia (*i.n.*, Text-fig. 1) are attached in Pheretima to the inner surface of the integument, or, in other words, to the somatic layer of the peritoneal lining of the cœlomic cavity. They are absent in the first two segments of the worm, but are present in all the succeeding segments. In each segment they extend all along the surface of the body-wall from the mid-ventral to the mid-dorsal line and are not arranged in any definite order, but are scattered promiscuously. It is seen, however, that they are more abundant midway in each segment on both sides of the line of setæ and are more sparse at the two ends of each segment, i.e. near the septa. They are best seen in specimens which have been fixed in acetic bichromate solution after they have been opened by a mid-dorsal incision and the flaps of skin pinned down.

The nephridia are extremely minute structures, hardly visible to the naked eye. They are attached to the body-wall only by means of their terminal ducts, i.e. in the same way as the septal nephridia are attached to the septa. The lobes and loops of these nephridia project out into the cœlomic cavity from the inner surface of the body-wall as V-shaped structures, the two limbs of the V being unequal in size and representing the straight lobe and the twisted loop of the septal nephridia (Pl. 7, fig. 7).

The number of these nephridia seems to vary in different segments. In those segments which possess septal nephridia the number of these integumentary nephridia is not very large; on counting I found about 250 nephridia in the thirtieth and about 200 in the thirty-ninth segment. But in the segments 14, 15 and 16, where the septal nephridia do not exist or only begin, and which are also incidentally the

clitellar segments, there is, so to speak, a "forest" of these integumentary nephridia, these being so numerous and so closely set as to cause the inner surface of the body-wall in these segments to look, under a lens, as if it were covered with dense fur (*F.I.N.*, Text-fig. 1). They are more than ten times as numerous on these three segments as on the preceding or succeeding segments; I was able to count as many as 220 on a piece of skin 2 mm. square from the fourteenth segment.

Like the septal nephridia, these integumentary nephridia also are separate from each other; each nephridium is a discrete structure and opens separately by its duct to the exterior on the skin (Pl. 7, fig. 7). There is no network of any kind formed by the tubules of separate nephridia, nor is there a connection between nephridia of successive segments by means of tubules perforating the septa, as suggested by Beddard (**2**, 1888). The number of nephridiopores on a segment will equal the number of nephridia in that segment. Beddard (**2**, 1888) states that the number of nephridiopores is greater anteriorly than posteriorly; it is very probable that he counted the nephridiopores on one of the three segments (fourteenth, fifteenth and sixteenth) which we have referred to above as possessing a "forest" of nephridia, and compared this number with the number of nephridiopores on any of the succeeding segments, and this led him to make the above-mentioned statement.

These nephridia are, as already mentioned, very minute; each is less than half the size of a septal nephridium; a nephridium of an average size when measured has the straight lobe about 100 μ in length and the long twisted loop about 182 μ in length. I have not been able to find any funnels in connection with these integumentary nephridia, but otherwise they are like the septal nephridia in their general structure.

(f) The Significance of the "Enteronephric" Type of Nephridial System.[1]

Benham (**4**, 1910), describing the excretory functions of the nephridia in Polychætes, writes: "Excretion, in the strict sense of the word, is carried out by the cells forming the wall of the nephridial tube; they remove waste materials from the blood distributed over the surface of the organ. But, in addition, there is a removal from the cœlom, by means of the funnel, of any dead or dying cœlomic corpuscles, which in their turn have eaten up or otherwise destroyed foreign bodies (such as Bacteria, etc.) that may have entered the animal." In Pheretima also, the septal nephridia have a copious blood-supply and possess cœlomic funnels with nephrostomes; we may therefore safely assume that here also as in Polychætes the nephridia discharge the function of excreting waste materials both from the blood and the cœlomic fluid. In the case of other worms the nephridia open to the exterior and all the excretory products are got rid of through the nephridiopores on the skin. But what can be the meaning of the elaborate "enteronephric" type of nephridial system in Pheretima, in which the excretory ducts ultimately open into the lumen of the alimentary canal along almost its entire length and presumably discharge all the excretory products into the gut?

The previously recorded cases of nephridia opening into the front and hind ends of the gut have been explained, on the one hand, as being peptic in function (peptonephridia),

[1] [Mr. Karm Narayan Bahl has not entered upon any discussion concerning the significance of his remarkable discovery of "enteronephric" nephridia in relation to the commonly-accepted view that all Annelid nephridia are ectodermal. But it seems to be evident that the septal nephridia of Pheretima certainly cannot be developed from the ectoderm but must be mesodermal in origin, since we can hardly suppose that they are endodermal outgrowths. Mr. Karm Narayan, however, has recently informed me that he has been successful in collecting a large number of Pheretima embryos and hopes to be able to ascertain the exact mode of development of the septal and other nephridia.—W. N. F. Woodland.]

and compared, on the other, with the respiratory trees of Bonellia and its allies and with the Malpighian tubes of the Arthropoda (Beddard, 3, 1895). Evidently we cannot explain away the segmentally arranged openings of this "enteronephric" system into the lumen of the gut in either of these two ways. These segmental openings must have a deeper significance. It has been suggested to me by Dr. Woodland that this enteronephric system is probably an adaptation for conservation of water in a tropical worm like Pheretima. This genus is Oriental as well as Australian in distribution, but is rare in the Australian region. There is no doubt that these worms have to adapt themselves to a very wide variation in the conditions of moisture: the region they inhabit is subject to a prolonged period of drought alternating with a short period of abundant moisture during the monsoon rains. Normally there are three to four rainy months alternating with eight or nine dry months in a year.

On à priori grounds, we must conclude that the excretory matters removed from the blood and the cœlomic fluid pass in a state of solution into the lumen of the gut viâ the system of ducts connected with the septal nephridia. In the intestine, we must assume that the water containing excretory matter in solution is re-absorbed by the gut epithelium for the needs of the organism, while the solid excretory matters pass out of the body through the anus. We are thus crediting the gut epithelium with the power of separating water from the excretory matters dissolved in it and then re-absorbing this water. Although there is, as yet, no experimental evidence in favour of this hypothesis, still we might mention one or two points in regard to this hypothesis very briefly. It is stated by Thomson (17, 1906) that when an earthworm has been made to eat powdered carmine, the passage of these useless particles from the gut to the yellow cells, from the yellow cells to the body-cavity and thence out by the excretory tubes can be traced. If that be so, we must conclude that the gut epithelium of the earthworm takes up these carmine particles and passes them on to the yellow cells

—or in other words, the gut epithelium acts as an organ of excretion in removing the useless carmine particles from the intestine; this, again, is a commonly admitted property of the intestinal epithelium. But we have to go further and ask how it is that, while the intestinal epithelium absorbs the carmine particles, it does not also absorb the excretory matter which is poured into the intestinal lumen viâ the excretory ducts? Why is it that from these it takes up only water and lets go the solid waste matter? In order to get over this difficulty we must assume that, like the intestinal epithelial cells of man, these cells of the earthworm also exercise a sort of protective function dependent on that capacity for physiological selection by which the epithelia of the intestine, while they absorb certain substances, do not permit others to pass into them.

Another consideration is about the relative importance of the septal and the integumentary nephridia. The latter are small in size but enormous in numbers, and open directly to the exterior through the skin. But as these nephridia do not possess any funnels and are closed internally, we should conclude that water cannot pass out in any quantity through them, although it may diffuse though the walls of the nephridia. There is very little loss, therefore, through these integumentary nephridia, and we may presume that all water is re-absorbed and conserved by the worm.

4. The Nephridial System of some other Species of Pheretima.

Besides Pheretima posthuma, the nephridial system of which I have described in detail above, I have examined the nephridial systems of three other species of the genus Pheretima, namely, P. hawayana, P. heterochæta and P. barbadensis. In general outline the nephridial system in these three species of Pheretima is similar to that in Pheretima posthuma, but there are certain differences which I shall mention below.

(1) Pheretima hawayana.—This species also possesses

the three kinds of nephridia, namely, the septal, the pharyngeal and the integumentary. These nephridia are very similar in position and structure to those of P. posthuma. We may only note that the septal nephridia here are larger than those of P. posthuma; the funnel is identical in structure with that of the latter species, but the first part of the nephridial tube, which makes a bend before joining the main body of the nephridium, is much longer in this species than in P. posthuma; in the latter it measures, on an average, about 84 μ in length, while in P. hawayana it is generally more than 180 μ long.

The septal excretory canal running parallel to the dorso-lateral vessel does not lie near or in contact with the vessel as in P. posthuma, but is removed a good distance from it: I measured the distance to be about 165 μ in one and about 412 μ in another specimen. As a consequence of these two structures lying far apart from each other, the terminal nephridial ducts have a very much longer course to run on the septum to meet the septal canal than they have in P. posthuma. Moreover, as the dorso-lateral vessel is not attached to the septum as in P. posthuma, the nephridial ducts do not cross this blood-vessel at all. We may also note in passing that the septa of P. hawayana are much more muscular than the septa of P. posthuma, and therefore in the former the septal canal and the terminal nephridial ducts on the septum are obscured by the muscle-fibres, and it is only by a careful examination that these structures can be made out.

The integumentary and the pharyngeal nephridia are identical in structure with those in P. posthuma.

(2) Pheretima heterochæta and Pheretima barbadensis.—The nephridial system in these two species resembles very closely that of P. hawayana rather than that of P. posthuma; the septal excretory canal is separated a good distance from the dorso-lateral vessel and the free duct following the funnel is much longer than that in P. posthuma.

5. The Blood-supply of the Nephridia in Pheretima.

Benham (6, 1891) has described in detail the vascular supply of the nephridium of Lumbricus, and in general outline this description applies to the vascular supply of the nephridia of Pheretima, but there are a number of interesting points in which the blood-supply of the nephridia in the two cases differs, these differences being due, firstly, to the much larger number of nephridia present in Pheretima, and secondly, to the fact that the nephridia of Pheretima are of three different kinds situated in three different regions of the body.

As in Lumbricus, the ventral vessel in Pheretima gives off, in the posterior part of each segment, a vessel on each side, which we may call the parietal vessel (*p.v.*, Pl. 6, fig. 11). This vessel, soon after its origin, perforates the septum behind and runs along the middle line of the inside of the body-wall of the succeeding segment ventro-dorsally (e.g. the ventral vessel in the twentieth segment gives off a pair of parietal vessels which perforate the septum 20/21 on each side and distribute blood over the inside of the body-wall of the twenty-first segment). The parietal vessel as it perforates the septum gives off a septal branch (*s.b.*), which runs along the septum very near its attachment to the body-wall parallel and external to the dorso-lateral vessel. This last vessel, as shown in the diagram, is a commissural vessel in each segment, joining the subneural with the dorsal vessel (*dl.v.*, Pl. 6, figs. 1 and 11). I may add, in passing, that there is no direct connection between the ventral and subneural vessels as has been supposed by some authors to be the case.

Although it is a difficult matter to decide what course is taken by the blood outside the large median trunks, yet from a comparison with the course of blood in Lumbricus and also from a number of observations on the distribution of valves in the blood-vessels, I am led to believe that the blood passes to the nephridia from the ventral vessel, and that it is

brought back to the dorsal vessel from the nephridia by way of the dorso-lateral vessel and the subneural vessel. The parietal vessel, as mentioned above, runs along the middle line of the inside of the body-wall ventro-dorsally, and during its course gives off a number of branches which ramify over the area of the body-wall of the whole segment, the vessel terminating near the mid-dorsal line. Now the whole of the inside of the body-wall is covered over by a large number of integumentary nephridia, and thus these are supplied with blood from the branches of the parietal vessel which also supplies blood to the body-wall. We have already said that the parietal vessel gives off a septal branch (*s.b.*, Pl. 6, fig. 11) as it perforates the septum. This septal branch is rather difficult to make out in preparations of the septa, since it lies very near the outer edge of the septum, in which position it is very generally torn off in the removal of the septum; its origin from the parietal vessel and its extent along the septum can both be seen, however, in preparations in which the outer edge of the septum is intact and the parietal vessel perforating the septum is also included. The septal branch runs parallel to the dorso-lateral vessel and is about one-third the diameter of the latter. All the septal nephridia receive their blood-supply from the septal branch, which throughout its entire course gives off a large number of twigs (*tt*), each twig supplying a septal nephridium. The blood from each septal nephridium is returned by another minute vessel (*t't'*) which runs parallel to the first in the base of the nephridium, and which joins, along with others of its kind, the dorso-lateral vessel. Each septal nephridium (Pl. 6, fig. 12), therefore, has two vessels in its basal part; the first one arises from the septal branch and enters and brings blood to the nephridium (we might call this the afferent nephridial vessel, *tt*); the second brings back blood from the nephridium and leaves the nephridium to join the dorso-lateral vessel into which the blood is now poured (we might call this vessel the efferent nephridial vessel, *t't'*). In each septal nephridium both the afferent and efferent

vessels fork near the base of the nephridium, one branch of each fork entering the straight lobe and the other branch entering the twisted loop (Pl. 6, fig. 12). These branches are continuous at their distal ends (*dd*), and there are also cross connections between them during their course (*cc*). We may note that the afferent vessel and the two branches of its fork are generally empty or contain very little blood, while the efferent vessel and the branches of its fork are full of blood; similarly the septal branch contains very little blood, while its counterpart, the dorso-lateral vessel, is generally full; this phenomenon corresponds with the condition of arteries and veins found after death in the higher animals, and lends additional support to the assumption made that the septal branch and the afferent vessels carry blood to the nephridium, while the efferent vessel removes the blood from it and pours it into the dorso-lateral vessel. The dorso-lateral vessel also receives a large number of branches from the body-wall, which presumably bring back blood from the body-wall proper and also from the integumentary nephridia. Another way by which blood from the integumentary nephridia may be returned to the general blood-stream is by means of capillaries and twigs that join together to enter the subneural vessel in each segment. The septal branch also receives small branches from the skin which possibly replenish its supply of blood for the septal nephridia. To sum up, the parietal vessels supply blood to the integumentary nephridia and body-wall directly, and to the septal nephridia through their septal branches, while the blood is returned from the integumentary and septal nephridia to the dorso-lateral vessel and possibly to the subneural vessel also (to this only from the integumentary nephridia).

In the case of the pharyngeal nephridia the blood-supply is different. In the fourth, fifth and sixth segments the dorsal vessel gives off in each segment a pair of branches, the branch of each side supplying the pharyngeal nephridia and the septa. In a freshly-killed worm in which the dorsal

vessel is still pulsating, one can easily see the flow of blood from the dorsal vessel to the pharyngeal nephridia through the branches referred to above. The blood is collected from these pharyngeal tufts of nephridia by capillaries, which unite together and open ultimately into the lateral œsophageal vessels which are situated ventro-laterally to the œsophagus, one on each side, and from which the blood goes into the blood-stream viâ the supra-intestinal vessel and the subneural. When a worm is opened some time after its death, it is always seen that the branches from the dorsal vessel are empty, while the branches carrying blood to the lateral œsophageal vessels and the latter themselves are full of blood.

6. The Intersegmental Septa in Earthworms.

The intersegmental septa of earthworms have always been regarded as partitions, partly membranous and partly muscular, which stretch across from wall to wall of the body and correspond roughly in their position to the grooves which divide the body externally into somites. The septa are perforated by the gut, the dorsal and the ventral vessels and also by the nerve-cord; the partitioning of the cœlom is incomplete around these structures in most earthworms, and there is free communication from one end of the body to the other for the cœlomic fluid. Except for holes and slits round the nerve-cord and other structures mentioned above, there is no record of any definite apertures, so far as I know, on the septa of earthworms. As a matter of fact, very little interest seems to have attached to the structure and disposition of septa as they had nothing peculiar about them, and they are dismissed in descriptions usually in a line or two. An interesting feature about these intersegmental septa presents itself, however, in Pheretima posthuma and other species of the same genus, which has been described here, I believe, for the first time: it is the presence of a large number of definite apertures each with a sphincter round it. In the

following paragraphs I shall provide a description of the septa in Pheretima posthuma, together with an account of these sphinctered apertures, and then compare these features with those of other species and genera that I have examined, and lastly, I shall discuss the possible significance of these sphinctered apertures in the septa of Pheretima.

(I) The Intersegmental Septa in Pheretima posthuma.—Beginning from the anterior end we find that the first definite septum lies between the fourth and fifth segments, the body-cavity of the first four segments being undivided or continuous, although it is traversed by a number of muscular strands passing from the buccal cavity and the pharynx to the body-wall. This first septum is thin and membranous, but the following five septa are very thick and muscular and resemble the intersegmental septa of Lumbricus. These separate the segments 5 and 6, 6 and 7, 7 and 8, 8 and 9 or 9 and 10, and 10 and 11 from each other; between the eighth and tenth segments there is always one septum; sometimes there is one between the eighth and ninth segments and septum 9/10 is missing, and vice versâ; both these septa are never present in the same worm. It happens that the lines of attachment of these septa on the alimentary canal are considerably behind (posterior to) their lines of attachment on the body-wall, and therefore these septa are not transverse in position, but form five cones, one inside the other, with their apices directed posteriorly (Text-fig. 1). These septa are incomplete over the ventral nerve-cord which perforates them, but besides these perforations and those of the gut and blood-vessels, these septa are quite complete partitions with no apertures on them. They are very thick and are formed of muscle-fibres disposed obliquely in two sheets, and have muscular strands passing from their anterior and posterior surfaces to the body-wall or to other septa in order to support them and keep them in position.

Behind the first eleven segments in which we have the specially thick septa mentioned above there is a regular series of thin and membranous septa separating successive

segments from each other interiorly. The septa 11/12, 12/13 and 13/14 are complete like the first six, although thin and membranous, the last two being intimately attached to the walls of the "hearts" in the twelfth and thirteenth segments. The next septum, i.e. 14/15, however, is typical of all the septa that follow, and besides being thin and membranous in texture and incomplete over the nerve-cord like the preceding septa, it is specially characterised by the fact that it is riddled with holes over the greater part of its area. These holes or apertures are either oval or circular in outline and are scattered over the lateral parts of each septum, being absent from the dorsal and ventral regions and also from the inner and outer edges. Each of these apertures possesses a thick sphincter around it formed of non-striped muscle-fibres arranged in a concentric manner (Pl. 8, fig. 13).

These sphincter apertures of the septa vary considerably in size; in my preparations I have found them to measure from 8 μ to 1650 μ in diameter. Very likely the apertures with a small diameter are in a closed condition, while those with a larger diameter are open. The thickness of the sphincters varies from 9 μ to 28 μ; it is, as would be expected, greater in closed apertures than in open ones. As regards the number of these apertures on the septa, I counted as many as sixty-eight on the left half of the septum 15/16, including one of the largest diameter I have come across (1650 μ). The number of apertures on the septa diminishes towards the posterior end of the worm.

The incompleteness of the septa round the nerve-cord is formed by a large circular hole in each septum which surrounds the nerve-cord, and the wall of which is made up of a thick, strong sphincter, the ventral part of which is attached to the body-wall. It may be noted that besides this large hole round the nerve-cord there is no slit or hole round the other structures that pierce the septa, e.g. the gut and the blood-vessels, in Pheretima, the septa round these latter structures being quite complete in this genus.

(2) Septa in Other Earthworms.—The septa in the

other species of Pheretima that I have examined, i.e. P. hawayana, P. heterochæta and P. barbadensis, have much more of muscular tissue in them than the septa of Pheretima posthuma. Moreover, although the sphinctered apertures are present on the septa of these species, the number of these apertures is very small indeed as compared with those in P. posthuma. I have never seen more than one or two on each septum, though they were always of a large size. I examined specimens of several other genera of earthworms in order to see if the septa in them had sphinctered apertures, but could not find any. They are absent in the septa of Megascolex, Perionyx, Lumbricus and Eutyphœus—the genera I have examined for this purpose. It is thus evident that, so far as is known at present, the sphinctered apertures characterise the septa of Pheretima only.

(3) The Significance of the Sphinctered Apertures.—The sphinctered apertures, together with the incompleteness of septa around the nerve-cord, are apparently the means by which the cœlomic fluid is allowed to pass from one segmental chamber into another. It is quite easy to see the flow of the cœlomic fluid inside the body-cavity in a living worm which happens to be a little more transparent than others. The sphincter muscles round these apertures are à priori the means of closing these apertures and thus restricting the flow of the cœlomic fluid to particular segmental chambers, and this isolation of these particular segments would be complete so far as the flow of the cœlomic fluid is concerned when the sphincter round the nerve-cord also contracts and closes that passage. This restriction of the cœlomic fluid to particular segments would lead to a condition of turgidity in those segments and make the worm stiff. It has been suggested that this stiffness would be necessary for the worm in its ordinary locomotory movements either on the surface of the soil or in burrowing, since, for the leverage of a particular part of the body to the ground by means of setæ (the organs of locomotion) it would be necessary

to have that part turgid and stiff, as the setæ on a limp part would not be able to secure a firm hold on the ground. The situation of the setæ in the middle of each segment in the form of a ring is most appropriate for balancing, and I agree with Beddard (**5**, 1912) in thinking that "the ring of setæ would seem to be a character specially suited to an underground life, where there is an equal pressure all round the body, and where progression would seem, therefore, to be best attained by a continual leverage round the circular body."

But why the sphinctered apertures should be present only in Pheretima and not in Megascolex and Perionyx, which are also forms with perichætine setæ, I cannot say.

7. Summary.

(1) There are three distinct kinds of nephridia in Pheretima posthuma and other species of the genus, namely, the septal, the pharyngeal and the integumentary, named according to the position they occupy in the worm; they differ from each other in size and also in respect of the place of opening of their ducts.

(2) Each nephridium is a separate and discrete structure and there is no network of any kind, and therefore the terms "plectonephric" and "diffuse" are inapplicable to these nephridia, although the term "micronephridia" can be retained.

(3) The integumentary nephridia are very minute and are hardly visible to the naked eye. Each of them has its own separate duct opening separately to the exterior on the skin. Each segment has about 200 to 250 of them. The pharyngeal nephridia occur in paired tufts lying at the sides of the œsophagus in the fourth, fifth and sixth segments; these nephridial tufts have three pairs of ducts, one in each segment, which open into the buccal cavity and the pharynx in the second and fourth segments.

(4) The septal nephridia are attached to both sides of the

septa ; they do not open on the skin, but are connected with an elaborate system of ducts which ultimately open into the lumen of the intestine mid-dorsally at segmental intervals. The system of ducts and openings is perfectly segmental in arrangement, and consists of a pair of septal excretory canals on each septum which open into a pair of supra-intestinal excretory ducts lying in the mid-dorsal line of the worm above the dorsal wall of the gut, these ducts communicating with the lumen of the intestine at each intersegmental place by means of a narrow ductule. This last feature is characteristic of this type of nephridial system, and the latter has therefore been termed the " enteronephric " type of nephridial system.

Each septal nephridium has a remarkable feature in that it lies—the funnel and all—wholly within the bounds of a single segment. The septal canals, the supra-intestinal ducts and their openings into the lumen of the gut have been described here for the first time, and the segmental character of the nephridial system of Pheretima, which was denied by Beddard, has now been established.

(5) The enteronephric nephridial system is probably a device for the conservation of water in this tropical genus, the gut-epithelium reabsorbing the water of the excretory fluid while letting the solid excretory matters pass out through the anus along with the fæces.

(6) Each nephridium in Pheretima, like that in Lumbricus, is connected with two blood-vessels, one bringing blood to it and the other taking away the blood. The septal and the integumentary nephridia are supplied with blood from the ventral vessel through the parietal vessel and the septal branch, and the blood is returned from these nephridia to the general blood-stream viâ the dorso-lateral vessel and the subneural vessel. The pharyngeal nephridia receive their blood-supply from the dorsal vessel, and the blood is returned from them to the lateral œsophageal vessels.

(7) The intersegmental septa in Pheretima posthuma and other species have definite, circular or oval apertures,

each with a sphincter muscle around it. It is suggested that by closing these apertures by means of sphincters there is a restriction of the cœlomic fluid to certain segments which become consequently turgid and stiff, and are thus able to help the setæ in having a firm hold of the ground during the locomotory movements of the animal; this turgidity of the part of the body applying setæ on to the ground seems necessary, since a limp part cannot fix its setæ on the substratum on which the worm moves.

8. Technique and Material.

Worms both for dissection and section-cutting were narcotised in weak alcohol (10 per cent. to 15 per cent.) for fifteen minutes or thereabouts. This method is much more useful than narcotising with chloroform, since the worms with this method do not contract at all, but die in a quite flaccid condition, and can easily be stretched to the utmost. The method of fixation most successfully employed for nephridia of all the three kinds as well as the intersegmental septa was immersion in acetic bichromate (3 per cent. potassium bichromate added to 5 per cent. glacial acetic acid) for forty-eight hours or more. Before fixing, however, the nephridia were fully exposed by opening the worms and pinning down the flaps of skin; a further precaution was found necessary in the fixation of these nephridia, and that was to wash off all cœlomic fluid before putting the worms in the fixative, as otherwise the cœlomic fluid coagulates near the nephridia and renders the fixation of the latter imperfect. In order to get the septa fully stretched they should be exposed by making a mid-dorsal incision in the worm, and pinning the flaps of the skin at intervals of five or six segments in such a way as to keep the intermediate four or five septa on stretch, but not to tear them at all. In this stretched condition the septa should be kept in the fixative for a week or two, after which time they become quite hardened and crisp, and can be removed very easily from their attachment with the body-wall and the wall of the gut. Metallic dishes should not be

used for preserving these various structures in bichromate; glass dishes or enamelled pie-dishes with the bottom filled up with hard paraffin answer the purpose very well.

For sectioning worms were fed on moist blotting-paper for a fortnight or thereabouts, after which time the gut is quite free of earth, and can be sectioned without injuring the razor. The sections were stained in the usual way with Delafield's hæmatoxylin, differentiated with acidulated water as recommended by Thapar (**16**, 1918), and "blued" with ammonia vapour after dehydration and clearing. For staining individual nephridia, I found a very weak solution of Delafield's hæmatoxylin followed by acidulated water very useful—even better than borax-carmine and acid alcohol; these hæmatoxylin preparations were very helpful in the investigation of the structure of the funnel, and specially the exact course of the nephridial tube in the body of the nephridium.

For a demonstration of the long terminal nephridial ducts and their openings into the septal excretory canals as well as of the commencement and extent of the latter, preparations stained with either borax-carmine or hæmatoxylin were made of the entire septa, and also a series of longitudinal sections was taken through six segments of the body-wall to which septa were still attached. In these sections I could follow the nephridial ducts from the place where they leave the nephridia to the point where they enter the septal excretory canal. I also incidentally came across many longitudinal sections of funnels in these preparations which were very helpful in ascertaining their structure.

The connections of the septal canals with the supra-intestinal excretory ducts were seen in preparations of the upper parts of the septa together with the supra-intestinal ducts, the last having been dissected out under a Zeiss binocular microscope. Similarly the ducts of the pharyngeal and the septal and integumentary nephridia themselves were also dissected under the binocular microscope, which was very helpful all along.

The segmental openings of the supra-intestinal excretory

ducts into the lumen of the intestine were identified in serial sections 6 μ in thickness passing through seven segments of the intestine.

Besides Pheretima posthuma, the species common in Allahabad, I have also examined three other species of Pheretima, namely, P. heterochæta (Mchlsn.), P. hawayana (Rosa) and P. barbadensis, specimens of which were kindly sent to me by Col. Stephenson from Lahore. Specimens of Lumbricus, Perionyx, Eutyphœus and Megascolex were also examined for their septa.

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EXPLANATION OF PLATES 6, 7 AND 8.

Illustrating Mr. K. N. Bahl's paper "On a New Type of Nephridia found in Indian Earthworms of the Genus Pheretima."

Fig. 1 (Pl. 6).—A diagrammatic representation of the septal nephridial system and its relative position in Pheretima posthuma. Three segments are shown, and part of the skin on the left side of the posterior (third) segment has been cut and reflected forwards so as to lie on the second segment, in order to expose the various structures. *b.w.*, body-wall; *b.w.*, body-wall cut and reflected forwards; *i.s.*, intersegmental septum; *s.a.*, sphinctered apertures; *d.v.*, dorsal vessel; *si.e.d.*, supra-intestinal excretory ducts; *g.*, gut; *ty.*, typhlosole; *v.v.*, ventral vessel; *sn.v.*, subneural vessel; *dl.v.* dorso-lateral vessel or the "septal loop"; *s.e.c.*, septal excretory canal; *t.n.d.*, terminal nephridial ducts; *s.n.*, septal nephridia; *si.v.*, septo-intestinal vessel. × cir. 17.

Fig. 2 (Pl. 7).—A septal nephridium showing the course of the nephridial tubule and its "ciliated tracts." *a–a'*, the first ciliated tract; *b–b'*, the second, *c–c'*, the third, *d–d'*, the fourth ciliated tract; *x*, the place of entrance and exit of the nephridial tube; *b.c.t.*, the "brown ciliated tube"; *o.l.*, the outer loop and *i.l.* the inner loop in the straight lobe; *p.l.*, the proximal limb, and *d.l.* the distal limb of the twisted loop; *f.*, funnel. × 220.